BIOGRAPHICAL SKETCH

Provide the following information for the key personnel in the order listed for Form Page 2. Follow the sample format for each person. DO NOT EXCEED FOUR PAGES.

NAME Raymond M. Welsh, Ph.D.

POSITION TITLE

Professor of Pathology, Molecular Genetics & Microbiology

INSTITUTION AND LOCATION	DEGREE (if applicable)	YEAR(s)	FIELD OF STUDY
University of Massachusetts, Amherst	B.S.	1967	Microbiology
University of Massachusetts, Amherst	Ph.D.	1972	Micro/Virology
University of Kansas, Lawrence	Post-Doc		Micro/Biochemistry
Scripps Clinic & Research Foundation, La Jolla, CA	Post-Doc		Virology/Immunology

A. Positions and Honors.

Positions and Employment

Visiting Assistant Professor of Microbiology, Univ. of Kansas, Lawrence, KS; Dept. of 1972-1973 Microbiology

Assistant Member, Scripps Clinic and Research Foundation, La Jolla, CA; Dept. of 1975-1980

Immunopathology

1979 Visiting Scientist, Karolinska Institute; Scripps Clinic, 1987.

1980 Adjunct Associate Professor of Pathology, Univ. California at San Diego Medical School, Dept.

of Pathology,

Associate Professor of Pathology, Molecular Genetics and Microbiology, Univ. Mass. Medical 1980-1985

School, Worcester, MA

1985-Present Professor of Pathology, Molecular Genetics and Microbiology, Univ. Mass. Medical School, Worcester, MA

Honors, Editorial Boards, and Advisory Groups:

Recipient of RCDA AI-00253 (1978-1983); Editorial Boards: J. Immunol. (1982-1986; 1997-present) Section Editor (2001); Proc. Soc. Exp. Biol. Med. (1978-1987); J. Virol. (1986-1989; 1991-present; Editor for Immunology and Pathogenesis1998-present); Natural Immunity Cell Growth Regulation (1984-2000); J. Natl. Cancer Inst. (1987-1991); J. Exp. Med. (1995-present); Virology (1996-present); Study Sections: American Cancer Society (National) Immunology and Immunotherapy Section (1988-1991); American Cancer Society (Massachusetts)(1981-1991), Chairman (1985-1991); State of California AIDS Task Force (1985-1996); NIH Virology (1991-1995).

B. Selected peer-reviewed publications (of 193 publications).

- Selin, L.K., K. Vergilis, R.M. Welsh and S.R. Nahill. 1996. Reduction of otherwise remarkably stable virusspecific cytotoxic T lymphocyte (CTL) memory by heterologous viral infections. J. Exp. Med. 183:2489-2499.
- Zarozinski, C.C. and R.M. Welsh. 1997. Minimal bystander activation of CD8 T cells during the virus-induced polyclonal T cell response. J. Exp. Med. 185:1629-1639.
- Tay, C.-H. and R.M. Welsh. 1997. Distinct organ-dependent mechanisms for the control of murine cytomegalovirus infection by natural killer cells. J. Virol. 71:267-275.
- Ciupito, A.T., M. Petersson, C.L. O'Donnell, K. Williams, S. Jindal, R. Kiessling and R.M. Welsh. 1998. Immunization with an LCMV peptide mixed with heat shock protein 70 results in protective anti-viral immunity and specific CTLs. J. Exp. Med. 187:685-691.

- Szomolanyi-Tsuda, E., Q.P. Le, R.L. Garcea, and R.M. Welsh. 1998. T cell-independent IgG responses in vivo are elicited by live virus infection, but not by immunization with viral proteins or virus-like particles. J. Virol.72:6665-6670.
- Varga, S.M., and R.M. Welsh. 1998. Cutting Edge: Detection of a high frequency of virus-specific CD4+ T cells during acute infection with LCMV. J. Immunol. 161:3215-3218.
- Lin, M.Y., and R.M. Welsh. 1998. Analysis of the stability of T cell receptor (TCR) repertoire usage during lymphocytic choriomeningitis virus (LCMV) infection of mice. J. Exp. Med. 188:1993-2005.
- Lohman, B.L., and R.M. Welsh. 1998. Apoptotic regulation of T cells and absence of immune deficiency in virus-infected IFN-y receptor knock-out mice. J. Virol. 72:7815-7821.
- Selin, L.K., S.M. Varga, I.C. Wong, and R.M. Welsh. 1998. Protective heterologous antiviral immunity and enhanced immunopathogenesis mediated by crossreactive memory T cell populations. J. Exp. Med. 188:1705-1715.
- Selin, L.K., M.Y. Lin, K.A. Kraemer, D.M. Pardoll, J.P. Schneck, S.M. Varga, P. Santolucito, A.K. Pinto, and R.M. Welsh. 1999. Attrition of T cell memory: selective loss of LCMV epitope-specific memory CD8 T cells following infections with heterologous viruses. Immunity 11:733-742.
- Welsh, R.M., T.G. Markees, B.A. Woda, K.A. Daniels, M.A. Brehm, J.P. Mordes, D.L. Greiner, A.A. Rossini. 2000. Virus-induced abrogation of transplantation tolerance induced by donor-specific transfusion and anti-CD154 antibody. J. Virol. 74:2210-2218.
- Zarozinski, C.C., J.M. McNally, B.L. Lohman, K.A. Daniels, and R.M. Welsh. 2000. Bystander sensitization to activation-induced cell death as a mechanism of virus-induced immunosuppression. J. Virol. 74:3650-3658.
- Selin, L.K., P.A. Santolucito, A.K. Pinto, and R.M. Welsh. 2001. Innate immunity to viruses: control of vaccinia virus infection by γδ T cells. J. Immunol. 166:6784-6794.
- Daniels, K.A., G. Devora, W.C. Lai, C.L. O'Donnell, M. Bennett, and R.M. Welsh. 2001. Murine cytomegalovirus is regulated by a discrete subset of natural killer cells reactive with monoclonal antibody to Ly49H. J. Exp. Med. 194:29-44.
- McNally, J.M., C.C. Zarozinski, M.Y. Lin, Brehm, M.A., Chen, H.D. and R.M. Welsh. 2001. Attrition of bystander T coells during virus-induced T cell and interferon responses. J. Virol. 75:5965-5976.
- Varga, S.M., Selin, L.K., and R.M. Welsh. 2001. Independent regulation of T cell memory pools: relative stability of CD4 memory under conditions of CD8 memory T cell loss. J. Immunol. 166:1554-1561.
- Welsh, R.M. 2001. Assessing CD8 T cell number and dysfunction in the presence of antigen. J. Exp. Med. 193:19-22
- Chen, H.D., A.E. Fraire, I. Joris, M.A. Brehm, R.M. Welsh, and L.K. Selin. 2001. Memory CD8+ T cells in heterologous antiviral immunity and immunopathology in the lung. Nat. Immunol. 2:1067-1076.
- Welsh, R.M. and L.K. Selin, 2002. No one is naive: The significance of heterologous T cell immunity. Nature Rev. Immunol. 2:417-426.
- Brehm, M.A., A.K. Pinto, K.A. Daniels, J.P. Schneck, R.M. Welsh, L.K. Selin, 2002. T cell immunodominance and maintenance of memory regulated by unexpectedly cross-reactive pathogens. Nature Immunol. 3:627-634
- Kim, S.-K., M.A. Brehm, R.M. Welsh, and L.K. Selin. 2002. Dynamics of memory T cell proliferation under conditions of heterologous immunity and bystander stimulation. J. Immunol. 169: 90-98.
- Brehm, M.A., T.G. Markees, K.A. Daniels, D.L. Greiner, A.A. Rossini, and R.M. Welsh. 2003. Direct visualization of cross-reactive effector and memory allo-specific CD8 T cells generated in response to viral infections. J. Immunol. 170:4077-4086.
- Wang, X.Z., S.E. Stepp, M.A. Brehm., H.D. Chen, L.K. Selin, and R.M. Welsh. 2003. Virus-specific CD8 T cells in peripheral tissues are more resistant to apoptosis than those in lymphoid organs. Immunity 18:631-642.
- Zipris, D., R.M. Welsh, J.P. Mordes, J.X. Xie, D.L. Greiner, and A.A. Rossini. 2003. Infections that induce autoimmune diabetes in BBDR rats modulate CD4⁺ CD25⁺ T regulatory cell populations. J. Immunol. 170:3592-3602.

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Principal Investigator/Program Director (Last, first, middle): Peacock, C.D., S-K. Kim, and R. M. Welsh. 2003. Memory T cell attrition: reduced capacity of bona-fide memory CD44^{hi} CD8⁺ T cells to respond to homeostatic and poly I:C-induced proliferation. J. Immunol. 171:0000-0000 (in press). 25306087.1

CURRICULUM VITAE

Raymond M. Welsh, Jr. S.S. No. 029-32-4074

Personal Data:

Date of birth:

December 28, 1945

Place of birth: Montague City, Massachusetts

Education:

University of Massachusetts, Amherst, B.S., 1967 (Microbiology)

University of Miami, Coral Gables, 1967-1968 (Microbiology)

Rensselaer Polytechnic Institute, Troy, N.Y., June 1971 December 1971 (Biology/Virology)

University of Massachusetts, Amherst, Ph.D., 1972 (Microbiology/Virology)

Professional Record:

Biologist, U.S. Army Natick Laboratories, Natick, MA, Feb. 1968-Sept. 1968.

Postdoctoral Research Assoc., Dept. of Microbiology, Univ. of Kansas, Lawrence, Kansas, Feb. 1972-Aug. 1973.

Visiting Assistant Professor, Univ. of Kansas, Aug. 1972-May 1973.

Research Fellow, Dept. of Exp. Pathol., Scripps Clinic and Research Foundation, La Jolla, CA, July 1973-Dec. 1973.

Assistant Member I Dept. of Immunopathol., S.C.R.F., July 1975-June 1977.

Assistant Member II Dept. of Immunopathol., S.C.R.F., July 1977-June 1980.

Visiting Scientist, Dept. of Tumor Biology, Karolinska Institute, Stockholm, Sweden, Oct. 1979-Dec. 1979.

Adjunct Associate Professor, Dept. of Pathology, Univ. of California at San Diego, La Jolla, CA, March 1980-Sept. 1980.

Associate Professor, Dept. of Pathology and the Dept. of Molecular Genetics and Microbiology, University of Massachusetts Medical School, Worcester, MA 01605, July

1980-June 1985.

Professor, Dept. of Pathology and the Dept. of Molecular Genetics and Microbiology, University of Massachusetts Medical School, Worcester, MA, 10605, July 1985-present.

Chairman, Interdepartmental Immunology and Virology program at UMMC (1992-1994; 1983-84); Vice-Chairman (1990-1992);

Visiting Scientist, Scripps Clinic, La Jolla, CA, 3/87-8/87.

Research Awards:

NIH AI-17672, Immunity and Virus Disease, 1974-2004, Principal Investigator

NIH NS-12428, Pathogenesis of MS and ALS, 1973-1980, Co Investigator.

NIH AI-00253, Maintenance of Chronic Virus Disease, 1978-1983, Research Career Development Award.

NIH CA-34461, Regulation of Natural Killer Cells, 1983-2005, Principal Investigator

NIH AM-35506, Virus-Induced Immunopathology, 1985-2004, Principal Investigator

NIH AI07349, Training in Immunology, 1992-2007, Principal Investigator (Training Grant).

Professional Organizations:

American Association of Immunologists American Society of Microbiology Society for Experimental Biology and Medicine

Boards and Committees:

Editorial Board, Journal of Immunology, (1980-1984) (1997-Present) Proceedings of the Society for Experimental Biology and Medicine, (1977-1988), Natural Immunity and Cell Growth Regulation (1983-present), Journal of Virology (1986-1988; 1991-present, Editor, 1997-present), J Natl Cancer Inst (1988-1990), Virology (1996-Present)

Arenavirus study group of the International Committee on Virus Nomenclature.

Grant Review study section of the Massachusetts Chapter of the American Cancer Society, 1981-1991; Chairman 1985-1991. Chairman of ACS Professional Scientific Advisory Committee (1994-1998)

Grant Review study section of the State of California AIDS Task Force, 1985-1996.

Grant Review National ACS study section: Immunology and Immunotherapy, 1988-1991.

NIH Virology Study Section, 1991-1995.

TEACHING EXPERIENCE

1968-69	Teaching assistant for general microbiology laboratory and for virology laboratory courses (Department of Microbiology, UMass, Amherst).
1972-73	Twice taught complete 40 lecture course in general microbiology to undergraduates (Department Microbiology, U. Kansas). Seminar course on slow virus infections (KU).
1980	Participated in laboratory course in virology for medical students at U.Cal., San Diego.
1981-present	Courses at the University of Massachusetts Medical Center:
	Medical student microbiology - an average of 9 lectures/year in immunology, virology, and bacteriology.
	Graduate student virology - coordinator and major lecturer each year - 20 hr. lectures per year.
	Graduate student advanced immunology - 3 hours of lectures/year.

BIBLIOGRAPHY

R.M. Welsh

Papers:

- 1. Welsh, R.M., R.S. Trowbridge, J.B. Kowalski, C.M. O'Connell and C.F. Pfau. 1971. Amantadine hydrochloride inhibition of early and late stages of lymphocytic choriomeningitis virus-cell interactions. Virology, 45:679-686.
- 2. Welsh, R.M. and C.J. Pfau. 1972. Determinants of lymphocytic choriomeningitis interference. J. Gen. Virol., <u>14</u>:177-187.
- 3. Welsh, R.M. 1972. Defective-interfering lymphocytic choriomeningitis virus. Doctoral dissertation, Univ. of Mass., Amherst.
- 4. Staneck, L.D., R.S. Trowbridge, R.M. Welsh, E.A. Wright and C.J. Pfau. 1972. Arenaviruses: cellular response to long-term in vitro infection with Parana and lymphocytic choriomeningitis viruses. Infect. Immun., 6:444-450.
- 5. Pfau, C.J., R.S. Trowbridge, R.M. Welsh, L.D. Staneck and C.M. O'Connell. 1972. Arenaviruses: inhibition by amantadine hydrochloride. J. Gen. Virol., 14:209-211.
- 6. Welsh, R.M., C.M. O'Connell and C.J. Pfau. 1972. Properties of defective lymphocytic choriomeningitis virus. J. Gen. Virol., <u>17</u>:355-359.
- 7. Pfau, C.J., R.M. Welsh and R.S. Trowbridge. 1973. Plaque assays and current concepts of regulation in arenavirus infections. In: F. Lehmann-Grube, ed., Lymphocytic Choriomeningitis Virus and Other Arenaviruses, Springer Verlag, New York, pp. 101-111.
- 8. Oldstone, M.B.A., R.M. Welsh and B.S. Joseph. 1975. Pathogenic mechanisms of tissue injury in persistent viral infections. Ann. N.Y. Acad. Sci., <u>256</u>:65-72.
- 9. Welsh, R.M., N.R. Cooper, F.C. Jensen and M.B.A. Oldstone. 1975. Human serum lyses RNA tumor viruses. Nature, <u>257</u>:612-614.
- 10. Welsh, R.M., P.A. Burner, J.J. Holland, M.B.A. Oldstone, H.A. Thompson and L.P. Villarreal. 1976. A comparison of biochemical and biological properties of standard and defective lymphocytic choriomeningitis virus. Int. Symp. on Arenaviral Infections of Public Health Importance, Atlanta, GA, W.H.O. Bull., 52:403-408.

- 11. Jensen, F.C., R.M. Welsh, N.R. Cooper and M.B.A. Oldstone. 1976. Lysis of oncornaviruses by human serum. 8th Int. Cong. of Assoc. for Comparative Res. on Leukemia, Copenhagen, Oct. 1975. Bibl. Haematol., 43:438-440.
- 12. Oldstone, M.B.A., L.H. Perrin and R.M. Welsh. 1976. Potential pathogenic mechanisms of injury in amyotrophic lateral sclerosis. <u>In</u>: J.M. Andrews, R.T. Johnson, M.A.B. Brazier, eds., Amyotrophic Lateral Sclerosis: Recent Research Trends, No. 19, Academic Press, New York, pp. 251-262.
- 13. Welsh, R.M., P.W. Lampert, P.A. Burner and M.B.A. Oldstone. 1976. Antibody-complement interactions with purified lymphocytic choriomeningitis virus. Virology, 73:59-71.
- 14. Welsh, R.M., F.C. Jensen, N.R. Cooper and M.B.A. Oldstone. 1976. Inactivation and lysis of oncornaviruses by human serum. Virology, 74:432-440.
- 15. Holland, J.J., L.P. Villarreal, R.M. Welsh, M.B.A. Oldstone, D. Kohne, R. Lazzarini and E. Scolnick. 1976. Long term persistent vesicular stomatitis virus and rabies virus infection of cells in vitro. J. Gen. Virol., 33:193-211.
- 16. Zinkernagel, R.M. and R.M. Welsh. 1976. H-2 compatibility requirement for virus-specific T-cell mediated effector functions in vivo. I. Specificity of T cells conferring antiviral protection against lymphocytic choriomeningitis virus is associated with H-2K and H-2D. J. Immunol., 117:1495-1520.
- 17. Cooper, N.R., F.C. Jensen, R.M. Welsh, Jr. and M.B.A. Oldstone. 1976. Lysis of RNA tumor viruses by human serum: Direct antibody independent triggering of the classical complement pathway. J. Exp. Med., 144:970-984.
- 18. Welsh, R.M. Jr. 1977. Host cell modification of lymphocytic choriomeningitis virus and Newcastle disease virus altering viral inactivation by human complement. J. Immunol., 118:348-354.
- 19. Oldstone, M.B.A., J. Holmstoen and R.M. Welsh, Jr. 1977. Alterations of acetylcholine enzymes in neuroblastoma cells persistently infected with lymphocytic chorioleningitis virus. J. Cell. Physiol., 91:459-472.
- Welsh, R.M., P.W. Lampert and M.B.A. Oldstone. 1977. Prevention of virus-induced cerebellar disease by defective-interfering lymphocytic choriomeningitis virus. J. Infect. Dis., <u>136</u>:391-399.
- 21. Merigan, T.C., M.B.A. Oldstone and R.M. Welsh. 1977. Interferon production during lymphocytic choriomeningitis virus infection of nude and normal mice. Nature, <u>268</u>:67-68.

- Welsh, R.M. and M.B.A. Oldstone. 1977. Inhibition of immunologic injury of cultured cells infected with lymphocytic choriomeningitis virus: Role of defective interfering virus in regulating viral antigenic expression. J. Exp. Med., 145:1449-1468.
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- Welsh, R.M., Jr. 1978. Cytotoxic cells induced during lymphocytic choriomeningitis virus infection of mice: 1. Characterization of natural killer cell induction. J. Exp. Med., 148:163-181.
- 25. Burton, P.R., J. Steuckemann, R.M. Welsh and D. Paretsky. 1978. Some ultrastructural effects of persistent infections by the rickettsia C. burneti in mouse L cells and green monkey kidney (Vero) cells. Infect. Immun., 21:556-566.
- Welsh, R.M. 1978. Mouse natural killer cells: induction, specificity and function. J. Immunol., 121:475-481.
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- Welsh, R.M. and M.J. Buchmeier. 1979. Protein analysis of defective interfering lymphocytic choriomeningitis virus and persistently infected cells. Virology, 96:503-515.
- 29. Cooper, N.R. and R.M. Welsh. 1979. Antibody and complement dependent viral ndutralization. Springer Semin. Immunopathol., <u>2</u>:285-310.
- Welsh, R.M. and R.W. Kiessling, 1980. Natural killer cell response to lymphocytic choriomeningitis virus in beige mice. Scand. J. Immunol., 11:363-367.
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- Welsh, R.M. and L.A. Hallenbeck. 1980. Effect of virus infections on target cell susceptibility to natural killer cell-mediated lysis. J. Immunol., <u>124</u>:2491-2497.
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- 35. Welsh, R.M. and R.W. Kiessling. 1980. Modification of target sensitivity to activated mouse NK cells by interferon and virus infections. <u>In</u>: R. Herberman, editor, Natural Cell-Mediated Immunity Against Tumors, Academic Press, New York, pp. 963-972.
- 36. Hansson, M., R. Kiessling and R.M. Welsh. 1980. Interaction between NK cells and normal tissue: definition of an NK-sensitive thymocyte population. <u>In</u>: R. Herberman, ed., Natural Cell-Mediated Immunity Against Tumors, Academic Press, New York, pp. 855-872.
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- 42. Hansson, M., R. Kiessling, B. Andersson and R.M. Welsh. 1980. Effect of interferon and interferon inducers on the NK sensitivity of normal mouse thymocytes. J. Immunol., 125:2225-2231.
- 43. Welsh, R.M. and W.F. Doe. 1980. Cytotoxic cells induced during lymphocytic choriomeningitis virus infection of mice. III. Natural killer cell activity in cultured spleen leukocytes concomitant with T cell dependent immune interferon production. Infect. Immun., 30:473-483.

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- 49. Biron, C.A. and R.M. Welsh. 1982. Activation and role of natural killer cells in virus infections. Med. Microbiol. Immunol., 170:155-172.
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- Welsh, R.M., C.A. Biron, J.F. Bukowski, S. Habu, M.V. Haspel, K. Holmes, K. Okumura and D.C. Parker. 1983. Regulation and role of natural cell-mediated immunity during virus infections. In: F.A. Ennis, ed., Human Immunity to Viruses, Academic Press, New York, pp. 21-41.
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- 57. Bukowski, J.F., C.A. Biron and R.M. Welsh. 1983. Elevated natural killer cell-mediated cytotoxicity, plasma interferon and tumor cell rejection in mice persistently infected with lymphocytic choriomeningitis virus. J. Immunol., 131:991-996.
- 58. Biron, C.A., G. Sonnenfeld and R.M. Welsh. 1984. Interferon induces natural killer cell blastogenesis in vivo. J. Leukocyte Biol., 35:31-37.
- 59. Biron, C.A., L.R. Turgiss and R.M. Welsh. 1983. Increase in NK cell number and turnover rate during acute virus infection. J. Immunol., 131:1539-1545.
- 60. Bukowski, J.F., B.A. Woda, S. Habu, K. Okumura and R.M. Welsh. 1983. Natural killer cell depletion enhances virus synthesis and virus induced hepatitis <u>in vivo</u>. J. Immunol., 131:1531-1538.
- 61. Welsh, R.M., C.A. Biron and J.F. Bukowski. 1984. The interplay between NK cells and virus infections. D. Schlessinger, ed., Microbiology-1984, American Society of Microbiology, Washington, D.C. pp. 320-323.
- 62. McIntyre, K.W., J.F. Bukowski and R.M. Welsh. 1985. Exquisite specificity of adoptive immunization in arenavirus-infected mice. Antiviral Res., 5:299-305.
- 63. Woda, B.A., M.L. McFadden, R.M. Welsh and K.M. Bain. 1984. Separation and isolation of rat natural killer (NK) cells from T cells with monoclonal antibodies. J. Immunol., 132:2183-2184.
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- 65. Bukowski, J.F., B.A. Woda and R.M. Welsh. 1984. Pathogenesis of murine cytomegalovirus infection in natural killer cell depleted mice. J. Virol., <u>52</u>:119-128.
- 66. Bukowski, J.F. and R.M. Welsh. 1985. Interferon enhances the susceptibility of virus-infected fibroblasts to cytotoxic T cells. J. Exp. Med., 161:257-262.
- 67. Bukowski, J.F., J.R. Warner, G. Dennert and R.M. Welsh. 1985. Adoptive transfer studies demonstrating the antiviral effect of natural killer cells in vivo. J. Exp. Med.,

161:40-52.

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- 69. Welsh, R.M., J.F. Bukowski and C.A. Biron. 1985. Regulation of virus infections by natural killer cells. Fed. Proc. (In Press).
- 70. Welsh, R.M., C.A. Biron, J.F. Bukowski, K.W. McIntyre and H. Yang. 1984. Role of natural killer cells in virus infections of mice. Surv. Synth. Pathol. Res., 3:409-431.
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